The braincases of two glyptosaurines (anguidae, Squamata) and anguid phylogeny

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JACK L. CONRAD[1] AND MARK A. NORELL[2]

ABSTRACT

Glyptosaurines are an extinct clade of anguids whose remains are common in many Holarctic Paleogene and Cretaceous deposits. Despite their extensive fossil record (comprised mainly of scutes) the braincase is poorly known. Here, we describe braincase morphology in two North American Eocene glyptosaurines, *Melanosaurus maximus* and *Helodermoides tuberculatus*. Although generally conservative in their braincase morphology compared with other anguids, these taxa and some other "higher" glyptosaurines possess a dorsally displaced parasphenoid rostrum. The anterior openings for the Vidian canals open almost directly ventral to the parasphenoid rostrum, and the internal carotids exit anteriorly almost directly dorsal to it. Our phylogenetic analysis recovers a monophyletic Glyptosaurinae nested within Anguidae as the sister taxon to a clade containing Gerrhonotinae and Anguinae. According to our analysis, "melanosaurins" are paraphyletic, *Placosaurus* is paraphyletic, and *Anniella* is the sister taxon to *Anguis*.

INTRODUCTION

Glyptosaurinae is an extinct Holarctic anguid radiation known from the Late Cretaceous and Paleogene. Although several studies have examined the osteology of this clade (e.g., Camp, 1923; Gilmore, 1928; Meszoely, 1970; Sullivan, 1979; Estes, 1983), few data exist about glyptosaurine braincase morphology. Because glyptosaurines are extinct, they are often ignored in systematic treatments of Anguidae.

Glyptosaurines are typically divided into the plesiomorphic "Melanosaurini" and the Glyptosaurini (Meszoely, 1970; Meszoely et al., 1978; Sullivan, 1979, 1986; Augé and Sullivan, 2006; Sullivan and Augé, 2006). "Melanosaurini" is usually considered to form a paraphyletic assemblage, a hypothesis sup-

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ported by a recent phylogenetic analysis (Conrad, 2008). Glyptosaurins possess tubercular, polygonal osteoderms on their skulls and bodies broadly similar in form to those of monstersaurs. More basal glyptosaurines (the "melanosaurins") typically possess larger, thinner plates on their skulls, more similar to those of other anguids such as gerrhonotines.

We recently discovered more than one-half of a braincase of *Helodermoides tuberculatus* (a glyptosaurin) that was previously identified as "basisphenoid?" as part of AMNH FR 6800. This specimen was collected by Glenn L. Jepsen in 1924 from the Chadronian (Lower Oligocene) of South Dakota. However, this specimen has remained largely undescribed and the braincase unrecognized, although Sullivan (1979) mentioned the skull and figured part of the specimen. The braincases of the holotype and paratype specimens of *Melanosaurus maximus* (a "melanosaurin") from the Wasatch Formation (Eocene) of Wyoming were originally described by Charles L. Gilmore in his seminal work on fossil squamates of North America. Here we describe these three glyptosaurine braincases. Our observations reveal an unusual morphology of the sphenoid in those Glyptosaurini and Melanosaurini for which braincases are known. We incorporated these new observations into a phylogenetic analysis. Our results further demonstrate the paraphyly of the so-called Melanosaurini and the monophyly of Glyptosaurinae and Glyptosaurini.

SYSTEMATIC PALEONTOLOGY

SQUAMATA OPPEL, 1811

SCLEROGLOSSA ESTES ET AL., 1988

ANGUIMORPHA FÜRBRINGER, 1900

ANGUIDAE GRAY, 1825

GLYPTOSAURINAE MARSH, 1872

Figures 1–2

DESCRIPTION OF BRAINCASES

Melanosaurus maximus GILMORE, 1928

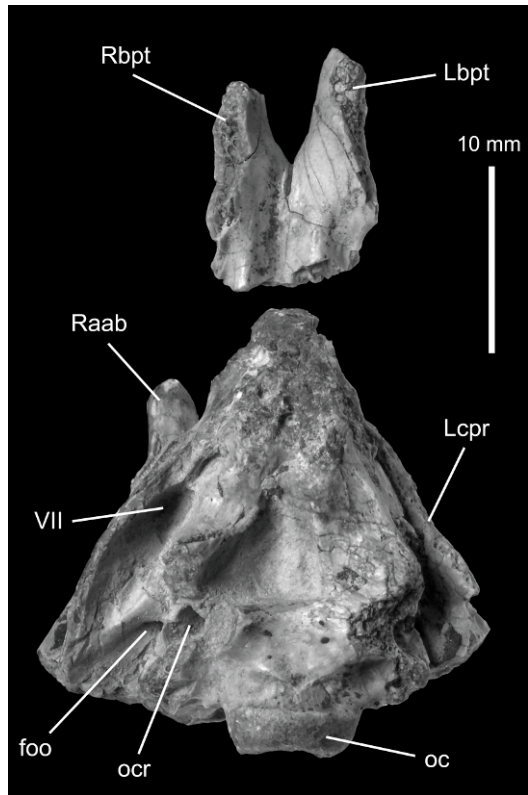LOCALITY AND AGE: AMNH FR 5168 and AMNH FR 5175 come from the Wasatch

Fig. 1. Ventral view of the braincase of the paratype of *Melanosaurus maximus* (AMNH FR 5175) with the anteroventral part of the sphenoid broken off, in ventral view. Note the narrow space between the basipterygoid processes anteriorly. Anatomical abbreviations in appendix 3.

Formation in Big Horn County, Wyoming, and are of Early Eocene age.

PRESERVATION: The braincase of the holotype (AMNH FR 5168) is articulated to the rest of the skull. Consequently, only the ventral surfaces of the sphenoid and basioccipital, part of the damaged otooccipitals, and the ventral parts of the prootics are visible. The paratype (AMNH FR 5175) (fig. 1) includes a disarticulated skull in which the braincase is isolated from the surrounding skull bones. Both braincases are damaged. The left paroccipital process is largely complete in AMNH FR 5168. The sphenooccipital tubercle is best preserved on the right side in AMNH FR 5168, but is damaged. The prootics are damaged in AMNH FR 5175 such that the anterior housing of the anterior
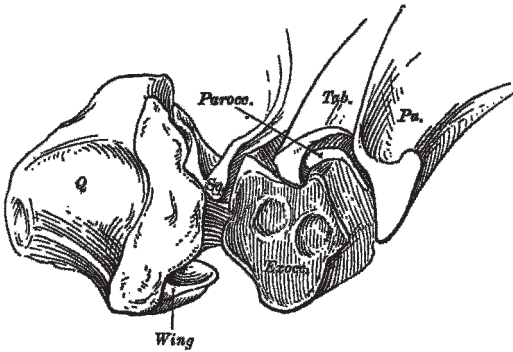
Fig. 2. Dorsolateral view of the left jaw suspensorium of *Melanosaurus maximus* (AMNH FR 5168) illustrating an element of uncertain homology, but labeled "parocc." in the figure. It may be part of the posterior process of the prootic (see text). Abbreviations for this figure: Exoc., exoccipital; Pa., parietal; Parocc, paroccipital; Q., quadrate; Sq., squamosal; Tab., supratemporal (tabular of Camp, 1923). After Camp, 1923.

semicircular canals and the crista alaris prootica are either not preserved or not visible in either specimen. Because the anterodorsal part of the sphenoid is damaged or hidden in the available material, the morphology of structures such as the dorsum sella and hypophyseal fossa cannot be determined. Both specimens retain the basipterygoid processes on the sphenoid, with minor damage. However, the anterior part of the sphenoid is damaged in AMNH FR 5175 and the basipterygoid processes have been separated from the rest of the braincase. Most of the remainder of the braincase is well preserved.

SPHENOID: The compound structure composed of the fused parasphenoid and basisphenoid is termed the sphenoid (Bever et al., 2005a). The basipterygoid processes are proximodistally very short, but their pterygoid articular surfaces are extremely broad. Each pterygoid facet is a medially concave elongate oval. It narrowly clasped the pterygoid in that it overlapped the pterygoid somewhat dorsally and ventrally. Unlike the condition observed in most extant anguids, the base of the basipterygoid process is unconstricted and there is very little "neck" to the basipterygoid process. The posterior part of the pterygoid facet of the basipterygoid process is only slightly expanded, so that it is nearly contig-

uous with the base of the process. The basipterygoid process extends well anterior to the anterior margin of the main body of the sphenoid. The interpterygoid vacuity is very narrow and the basipterygoid processes lie adjacent to each another, the space between them is a narrow "V" shape in ventral view (fig. 1). Thus, although the basipterygoid processes are short, they are well developed and extend far forward. This condition is in contrast to the abbreviated basipterygoid processes of mosasauroids and amphisbaenians (taxa also characterized as having short basipterygoid processes). Importantly, both *Melanosaurus maximus* and *Helodermoides tuberculatus* show a derived condition of the anterior part of the sphenoid, in which the parasphenoid rostrum lies dorsal to the medially placed anterior openings of the Vidian canal. This will be described in more detail below.

The paratype (AMNH FR 5175) is broken and the anteroventral part of the sphenoid is separate from the rest of the element (fig. 1). In dorsal view, this broken anterior portion shows the anterior projection of the Vidian canal. The left side shows the course of the anterior component of the Vidian canal and the right preserves the point of separation where the common Vidian canal splits into a cranial carotid canal and the anterior Vidian canal. This occurs posterior to the level of the posterior margin of the pterygoid facet, near the posterior end of the common Vidian canal.

Both the holotype and paratype show remnants of the sphenoid-basioccipital suture. It is an anteriorly arching contact on the ventral surface of the skull. Posterolateral flanges of the sphenoid narrowly overlay the basioccipital ventrolaterally and extend onto the bases of the spheno-occipital tubercles. The exact position of the posterior opening of the Vidian canal is uncertain, but it appears to have exited at the sphenoid-prootic contact.

BASIOCCIPITAL: The basioccipital is robust laterally, but relatively thin anteromedially. It possesses robust spheno-occipital tubercles. Co-ossification between the basioccipital and otooccipitals has obscured the suture between these two bones on the occipital condyle, but it appears that the basioccipital makes up most of the occipital condyle.

In both specimens the ventral floor of the braincase at the anterior margin of the basioccipital is collapsed. This is most apparent in AMNH FR 5175, but is present in both specimens. The anterior and middle braincase floor of many squamates is thin relative to surrounding areas of the braincase. For example, the posterior part of the sphenoid and anterior part of the basioccipital are thin in *Shinisaurus crocodilurus* (Conrad, 2004; Bever et al., 2005a, b) and *Heloderma suspectum* (Bonine, 2005). Some anguids possess a similar thinning of the braincase floor in tandem with a dorsally projecting fossa on the ventral surface of the sphenoid and/or basioccipital (see, for example, coronal slices 550–577 in Maisano, 2006) (Criley, 1968; Rieppel, 1980; Good, 1987; Maisano, 2006; personal obs.). Such a thin point may have been present in the basioccipital of *Melanosaurus maximus*, creating a weak area that collapsed during fossilization.

In both specimens the spheno-occipital tubercles are damaged. However, it is clear that they were robust, short, and posteriorly placed. The right spheno-occipital tubercle is mostly complete on AMNH FR 5168. Its distal tip seems to show an articular surface for an unfused epiphysis.

As noted by Gilmore, the occipital condyle is somewhat "reniform" (Gilmore, 1928: 141); as it is a ventrally convex arch in posterior view, with a slight dorsal concavity. Even so, the occipital condyle is single (rather than trilobed or tripartite). This morphology is consistent with most extant anguids, and with *Glyptosaurus sylvestris* (Middle Eocene of western U.S.; see Sullivan, 1986) and *Peltosaurus granulosus* (the other glyptosaurines for which the occipital condyle is known) (e.g., AMNH FR 1710).

SUPRAOCCIPITAL: The supraoccipital is present in both specimens, but is best preserved in AMNH FR 5175. Dorsoventral compression and some mediolateral compression of the skull make contacts between the otooccipitals, prootics, and supraoccipital obscure. This is further complicated by the apparent partial fusion between the prootics and otooccipitals. On the right side of the braincase, the supraoccipital has moved somewhat dorsally with respect to the right prootic, revealing the straight posterior suture between them.

The general form of the supraoccipital appears to be consistent with that of other anguimorphs. A triangular articular surface for the processus ascendens is preserved anteromedially. The apex of this triangle faces posteriorly and is contiguous with a midline ridge that becomes progressively less pronounced posteriorly and terminates about two-thirds of the way to the dorsal margin of the foramen magnum.

PROOTIC: Prootics are visible only in AMNH FR 5175. Both cristae alaris prootica have been lost and the bullae housing the anterior part of the membranous labyrinth are broken, so that the canals themselves, which are infilled by matrix, are visible. The posterior processes, which anteriorly and anterodorsally overlie the paroccipital processes of the otooccipital, are also broken, so that their posterior extent is unknown. The right prootic is more complete than the left.

The trigeminal notch is a deep incisure of the prootic posteroventral to the housing of the anterior semicircular canals and the anterior part of the membranous labyrinth. No supratrigeminal ridge is present. The inferior prootic process appears to be complete and is square anteriorly with an anteroventrally projecting anterior margin. Its contact with the sphenoid is damaged. However, the robust prootic crest (crista prootica) is well preserved posterior to the level of the exposed part of the Vidian canal. Its lateral portion curves ventrally, forming a dorsal recess. A single facial foramen (through which cranial nerve VII exits the braincase) is present within this recess at a level just anterior to the spheno-occipital tubercle (fig. 1). The posterior process overlies the otooccipital posteriorly and is partly fused to it.

OTOOCCIPITAL: Adult and subadult squamates are usually characterized by the fusion of the exoccipital and the opisthotic. This compound structure is referred to as the *otooccipital* (following recent usage, e.g., Maisano, 2001; Maisano et al., 2002; Conrad, 2004; Bever et al., 2005a; Maisano et al., 2006). The opisthotic portions of the otooccipitals in both specimens are generally less complete than the exoccipital portions. Both paroccipital processes have been shorn off near the level of the foramen magnum in

AMNH FR 5175. The left paroccipital process is more complete in AMNH FR 5168 and it was figured by Camp (1923) and Gilmore (1928) (see below) (fig. 2).

Most of the sutures between the otooccipitals and the basioccipital have been obliterated by co-ossification of the two bones, but the otooccipital contribution to the occipital condyle appears to be small relative to that of the basioccipital. The vagus foramen (communicating cranial nerve X) is well separated from a series of three hypoglossal foramina (for the exit of branches of cranial nerve XII). The crista tuberalis is damaged in both specimens, but its dorsal part is preserved in AMNH FR 5175 and is somewhat posterodorsally inclined. The occipital recess is well preserved and appears as a deep, narrow recess delimited posteriorly by the crista tuberalis, dorsally and anterodorsally by the crista interfenestralis, and anteroventrally by the swelling at the base of the spheno-occipital tubercle. Repreparation of AMNH FR 5175 has revealed the inner division of the occipital recess into the perilymphatic duct and the medial aperture of the recessus scala tympani (sensu Bever et al., 2005a; aquaeductus cochleae of Jollie, 1960 and round window niche of Wever, 1978). Dorsal to the crista interfenestralis, the fenestra ovalus opens posterolaterally.

The broken surface of the paroccipital process in AMNH FR 5168 has received some scrutiny in the past. Camp (1923) and Gilmore (1928) identified what they thought was a separate bony element of uncertain homology. Camp (1923) identifies this element as the paroccipital, but Gilmore (1928) suggests that it might be the same element as is present in some specimens of *Lacerta viridis*, citing Leydig as a source, but listing no specific study.

Dorsoventral compression of AMNH FR 5168 has dislocated many skull bones out of their natural articulation. The parietal and supraoccipital (tabulare of Gilmore, 1928) have been separated and the supraoccipital process of the parietal has been translated medially relative to the preserved part of the paroccipital process. Given this movement, it seems possible that the element in question might represent the posterior section of the posterior process of the prootic (the portion that typically anterolaterally overlies the paroccipital process).

HELODERMOIDES TUBERCULATUS DOUGLASS, 1903

LOCALITY AND AGE: AMNH FR 6800 comes from the Chadron Formation (Chadronian) in Badlands, South Dakota, and is of Lower (Early) Oligocene age.

PRESERVATION: A referred specimen of *Helodermoides tuberculatus*, AMNH FR 6800, consists of an incomplete skeleton, including a partly disarticulated skull with more than one-half of an articulated braincase. The braincase of this specimen has been labeled "basisphenoid?" since its discovery by Glenn L. Jepsen in 1924, but consists primarily of a sphenoid and basioccipital (the right basipterygoid process is damaged and the left is absent), a left prootic that lacks only the crista alaris prootica, and a left otooccipital that lacks only the distal part of the paroccipital process. The elements are preserved in articulation and exhibit very minor dorsoventral compression (figs. 3–5).

SPHENOID: The sphenoid is fused to the basioccipital and only a slight indication of the suture remains posteriorly. This sutural remnant occurs on the posteromedial margin of the posterolateral sphenoid processes and demonstrates that these posterolateral processes extended at least part way down the spheno-occipital tubercles of the basioccipital. Nearly complete fusion of the sphenoid, basioccipital, and prootic obscures the relationships of these three bones, indicating that this specimen was an adult. A faint suture remnant remains between the sphenoid and basioccipital posteriorly and demonstrates the presence of posterolateral processes of the sphenoid overlapping the base of the spheno-occipital tubercles. These narrow processes define the posterolateral margins of the braincase. The dorsolateral margin of this suture remains distinct near the posterior opening of the Vidian canal. Based on this suture, the posterior opening of the Vidian canal lies between the prootic and the sphenoid.

The basipterygoid processes are relatively more proximodistally elongate than in *Melanosaurus maximus*, but the lateral extent remains uncertain (fig. 3). As with
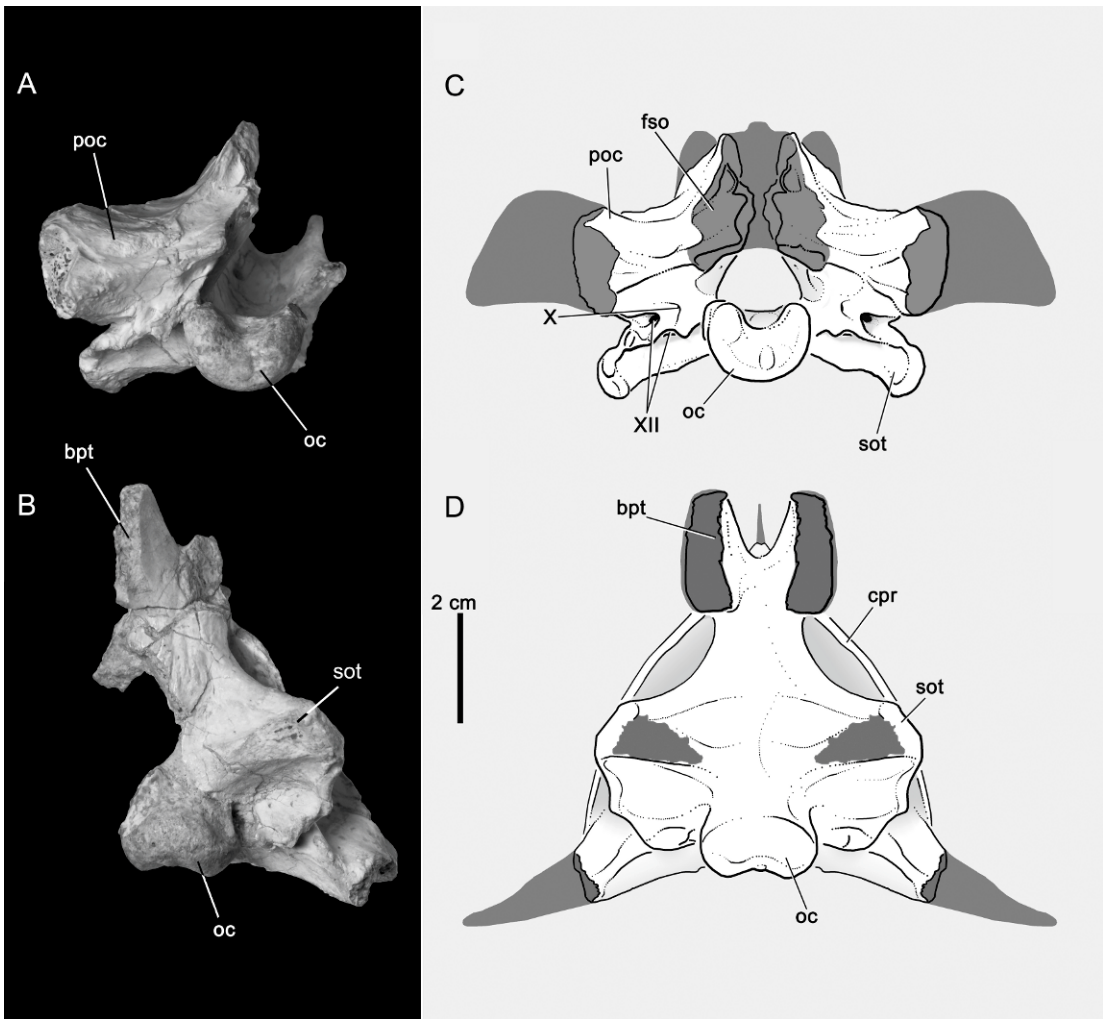
Fig. 3. Braincase of *Helodermoides tuberculatus* (AMNH FR 6800). Photos in (A) posterior and (B) ventral views. Reconstruction in (C) posterior and (D) ventral views. Note that elements known only from one side have been drawn bilaterally for the reconstruction and that the slight dorsoventral compression has been removed in the reconstruction. Elements not represented by remains are reconstructed as semiopaque shadows. Anatomical abbreviations in appendix 3.

Melanosaurus maximus, there is very little constriction at the base of the basipterygoid process and the anteromedial portions of the pterygoid facets approach the midline. In contrast to *Melanosaurus maximus*, *Helodermoides tuberculatus* has slightly more elongate basipterygoid processes. Only a small part of the crista prootica extends onto the sphenoid posterodorsally, and thus did not contact the basipterygoid process distally to enclose the lateral head vein.

The common Vidian canal opens posteriorly between the prootic and the sphenoid as in other anguids, and there is an entocarotid fossa as in non-anguine anguids. The anterior openings of the Vidian and cranial carotid canals are unusual in that they lie very close together. Rather than lying lateral to the parasphenoid rostrum, the anterior openings of the Vidian canals lie ventral to it (fig. 4). A robust anterior flange joins the anterolateral margin of the parasphenoid rostrum with the
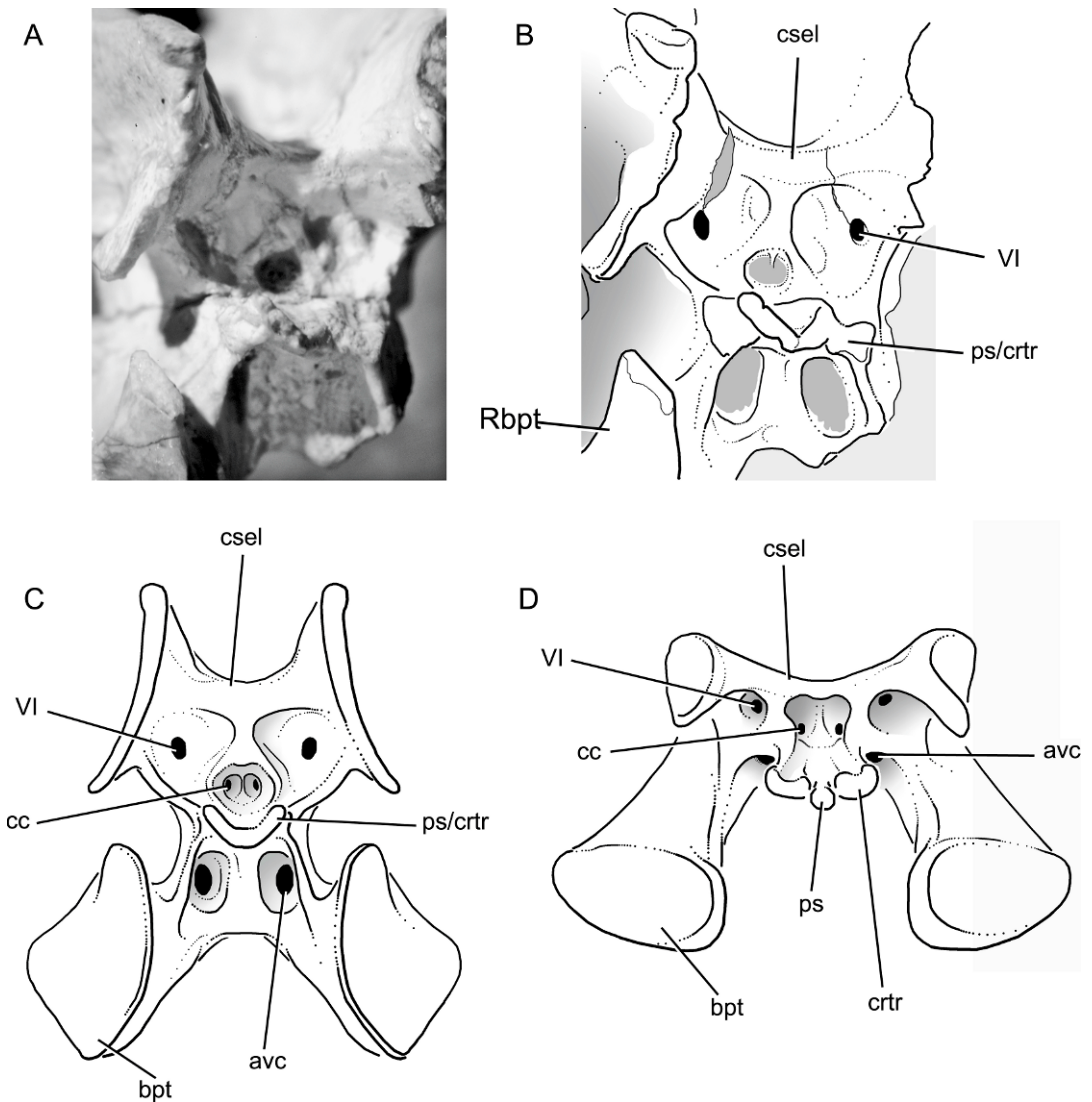
Fig. 4. Anterior view of the sphenoid in (A–C) *Helodermoides tuberculatus* (AMNH FR 6800) compared with (D) that of *Shinisaurus crocodilurus* (UF 57112). *Helodermoides tuberculatus* and some other glyptosaurines possess unusual sphenoid morphology. The margin of the parasphenoid rostrum (ps) is continuous with the cristae trabeculae (crtr) and positioned dorsal to the ventromedially placed anterior openings of the Vidian canal in *Helodermoides tuberculatus*. *Shinisaurus crocodilurus* possesses the more typical squamate condition in which the parasphenoid rostrum is distinct from the cristae trabeculae and both of these structures lie near the ventral midline of the braincase. Anatomical abbreviations in appendix 3.

anterodorsal border of the basipterygoid process, and forms the lateral margin to an anteriorly oriented Vidian fossa. The margin of the broad parasphenoid rostrum is continuous with the cristae trabeculae and forms the dorsal margin of this Vidian fossa (fig. 4). It is partly enclosed ventrally by the close proximity of the medial borders of the bases of the basipterygoid processes.

Dorsal to the anterior Vidian apertures, the parasphenoid rostrum and cristae trabeculae form a broad plate. Dorsal to this, and at midline, there is a small pituitary fossa (hypophyseal fossa). The joining of the two
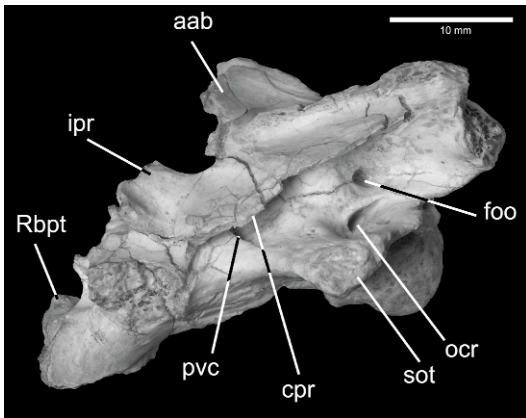
Fig. 5. Left lateral view of the braincase of *Helodermoides tuberculatus* (AMNH FR 6800). Anatomical abbreviations in appendix 3.

cranial carotid canals just posterior to the pituitary fossa forms a common cranial carotid canal that opens directly into the pituitary fossa. Large, mediolaterally broad retractor fossae lie lateral and dorsolateral to the pituitary fossa, and are separated from the latter by weak, yet distinct, crests.

The robust crista sellaris is arched posteriorly in dorsal view and arched strongly ventrally in anterior view. An abducens canal (for passage of cranial nerve VI) pierces the sphenoid. Its posterior opening occurs ventrolaterally, posterior to the level of the inferior process. The anterior opening for the abducens canal lies laterally within the retractor fossa, near the base of the inferior process.

The inferior process is dorsoventrally broad. Its ventral margin is free and extends somewhat ventrolaterally. This ventrolateral flange is not contiguous with the crista prootica (see below).

BASIOCCIPITAL: More than one-half of the basioccipital is preserved, but it is fused to surrounding bones. The dorsal surface of the basioccipital within the brain cavity is concave ventrally. Breakage of the basioccipital allows a clear view of its dorsoventral thickness near the midline. Although it has not broken or collapsed, as in the available *Melanosaurus maximus* specimens, the midline floor of the braincase in *Helodermoides tuberculatus* is very thin near the sphenoid-basioccipital contact.

The spheno-occipital tubercles are robust, although not particularly elongate, and posteroventrally and ventrolaterally oriented. The anterior margin of the spheno-occipital tubercle arches anteroventrally to its apex at the level of fenestra ovalus. From there, the margin of the spheno-occipital tubercle extends posterodorsally and is contiguous with the crista tuberalis.

As with *Melanosaurus maximus*, the occipital condyle is U-shaped or reniform. Its dorsal surface bears a distinct mid-ventral pit. The exact amount of basioccipital contribution to the occipital condyle is uncertain because of fusion to surrounding bones. The base of the occipital condyle is somewhat constricted forming a short neck. A broad ridge extends from the base of the occipital condyle onto the spheno-occipital tubercle.

PROOTIC: Only the left prootic is preserved, but it is relatively complete. The crista alaris prootica is damaged, but the rest of the element is well preserved (fig. 5). Although the ventral contacts with the sphenoid, basioccipital, and otooccipital cannot be identified because the sutures are fused, a clear suture lies dorsally between the posterior process of the prootic and the otooccipital.

The osseous housing for the anterior semicircular canal is intact and forms a broad anterior arch at the anterodorsal margin of the braincase. This would be amplified by the crista alaris prootica if the latter were well preserved. Posterior and medial to the anterior semicircular canal, the dorsal surface of the prootic retains a clear and well-preserved articular surface for the supraoccipital. This surface tapers anterolaterally and extends onto the dorsal surface of the otooccipital.

The deep, narrow trigeminal notch is bounded dorsally by the housing for the anterior semicircular canal and ventrally by the inferior process (fig. 5). The lateralmost margin to the trigeminal notch is a broad arc, but it is partly subdivided by a small, distinct, supratrigeminal process. The supratrigeminal process is damaged, but remains visible. It is posteromedially contiguous with a ridge that anteriorly bounds the acoustic recess.

The facial foramen (communicating cranial nerve VII) lies directly ventral to the anterior auditory foramen within the acoustic recess.

The large posterior auditory foramen lies well posterior and dorsal to the anterior auditory foramen along the anteroventral part of the tympanic bulla. The posterodorsal surface of the prootic is damaged and the supraoccipital is missing, so the exact location of the endolymphatic foramen cannot be determined. However, the canal is visible on the broken posterodorsal surface of the prootic, just dorsal to the tympanic bulla and the posterior margin of the posterior auditory foramen.

A large, robust crista prootica extends laterally and ventrally on the lateral surface of the prootic. It originates ventrolaterally on the sphenoid and extends posterodorsally onto the prootic and the posterior process of the prootic paroccipital process. It hides the facial foramen and the posterior opening of the Vidian canal in lateral view. The anterodorsal concavity formed by the crista, the prootic fossa, is very deep and extends nearly to the level of the trigeminal notch. The single facial foramen lies posteriorly within the deepest part of the prootic fossa, near the lateral swelling of the lagenar chamber (the ventral part of the external auditory bulla). The posterior margin of the crista prootica merges with the main body of the posterior process of the prootic. This process is rounded posteriorly and lies along the lateral surface of the otooccipital. A second distinct crest is also present on the dorsolateral surface of the posterior process (fig. 5), extending from the tip of the posterior process anteriorly to the trigeminal notch.

OTOOCCIPITAL: Only the left otooccipital is preserved. Its paroccipital process is incomplete, but the bone is otherwise well preserved. Only remnants of the sutures with the prootic and with the basioccipital remain distinct.

Both the fenestra ovalus and the occipital recess are deep and well preserved (fig. 5). The occipital recess is poorly defined, but the recessus scalae tympani is very distinct within the occipital recess. The occipital recess is separated from the fenestra ovalus by a short, distinct crista interfenestralis. Its posterior margin is formed by the crista tuberalis, and it gently grades away onto the spheno-occipital tubercle ventrally. The recessus scalae tympani is a narrow slit bordered anteriorly by the crista interfenestralis. The fenestra ovalus is about one-half the size of the recessus scalae tympani and is a subovoid opening at the junction of the prootic and otooccipital.

The robust crista tuberalis extends from the basioccipital, where it originates on the dorsal surface of the spheno-occipital tubercle, onto the otooccipital. Its dorsomedial terminus defines the ventromedial margin of the paroccipital process. The external hypoglossal foramina (communicating branches of cranial nerve XII) occur along the dorsolateral edge of the crista tuberalis, at the base of the paroccipital process. This area has been slightly compressed, but two hypoglossal foramina remain distinct and are clearly separated from the external opening of the vagus foramen (the conduit cranial nerve X through the braincase), which lies more dorsomedially, nearer the occipital condyle. The medial opening of the vagus foramen is preserved as a narrow slit at the posterior margin of the tympanic bulla. A series of three small hypoglossal foramina arranged in an anteroventral line are present ventral and posteroventral to the internal vagus foramen. The large perilymphatic foramen is present at the anteroventral tip of the line of hypoglossal foramina.

PHYLOGENETIC ANALYSIS

RECENT WORK

Although many analyses, both morphological (with and without fossils) and molecular, have focused on the evolution of platynotans (e.g., Pregill et al., 1986; Norell et al., 1992; Baverstock et al., 1993; Pianka, 1995; Lee, 1997; Fuller et al., 1998; Nydam, 2000; Ast, 2001; Pepin, 2001), relatively few have concentrated on Anguidae (but see Macey et al., 1997; Wiens and Slingluff, 2001). Perhaps because they are known only from fossil specimens, glyptosaurines have been included in the analysis in only a subset of those studies (Sullivan, 1979; Gauthier, 1982; Conrad, 2006, 2008).

Sullivan (1979) suggested that glyptosaurines were the most basal members of Anguidae, and that diploglossines and anguines were extant sister taxa (fig. 6A). By contrast, Gauthier (1982) suggests that gerrhonotines and diploglossines are extant sister taxa, that glyptosaurines are the outgroup to
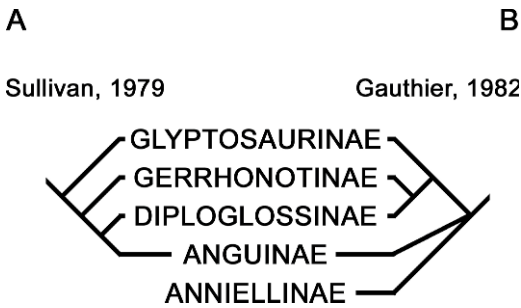
A

Sullivan, 1979

B

Gauthier, 1982

Fig. 6.   Phylogenetic relationships of Anguidae based on morphology as hypothesized by (A) Sullivan, 1979, and (B) Gauthier, 1982.
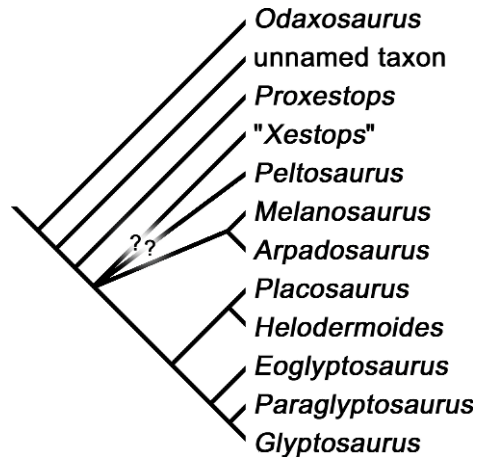

Fig. 7.   Cladogram of glyptosaurine as hypothesized by and presented in Sullivan (1986). Note that the specimens of *Eoglyptosaurus donohoei* are now assigned to *Glyptosaurus sylvestris* and *Proglyptosaurus huerfanensis* (Sullivan, 1989).

that clade, and that anguines and anniellines (consisting of *Anniella* and *Apodosauriscus minimus*) form an unresolved trichotomy with other anguids (fig. 6B).

Sullivan also addressed the interrelationships within glyptosaurines (Sullivan, 1986) and anguids (Sullivan, 1987). He suggested that *Odaxosaurus piger* (Upper Cretaceous of western United States; see Gilmore, 1928; Estes, 1964; Gauthier, 1982) is the basalmost member of a glyptosaurine lineage (Sullivan, 1986). Furthermore, he indicated that an "unnamed [and unidentified] taxon" and *Proxestops jepseni* (Upper Paleocene of western United States; see Gauthier, 1982) form successively more proximal outgroups to a clade containing melanosaurins and glyptosaurins (Sullivan, 1986) (fig. 7). Later, Sullivan (1987) addressed interrelationships within Anguinae, indicating that many of the "*Ophisaurus*" species together with *Parophisaurus pawneensis* (upper Lower Oligocene of western United States; see Sullivan, 1987) form a clade at the base of Anguinae and that *Machaerosaurus torrejonensis* (Upper Paleocene of western United States; see Gilmore, 1928; Gauthier, 1982) and *Pseudopus* (including the species *buttikoferi*, *gracilis*, *harti*, and *wegneri* according to Sullivan, 1987) were successively more proximal outgroups to *Ophisauriscus* and *Anguis*.

Recently, molecular analyses have focused on the evolutionary history of anguids and closely related taxa (Macey et al., 1999; Wiens and Slingluff, 2001) (fig. 8). These analyses support the placement of *Xenosaurus grandis* as the extant sister taxon to Anguidae, and

that Gerrhonotinae and Anguinae are monophyletic exclusive of Diploglossinae and *Anniella* (both species). Macey et al. (1999) suggested that *Anniella* was the sister taxon to other anguids, whereas Wiens and Slingluff (2001) suggested that *Anniella* is the sister taxon to diploglossines. Obviously these molecular analyses did not include fossil taxa (nor were they total evidence in the sense that they included any morphology), and therefore cannot address the positions of glyptosaurines within anguids or the relationships within glyptosaurines.

One recent analysis has approached this subject (Conrad, 2008). Conrad (2008) found gerrhonotines to be basal within Anguidae and that diploglossines and anguines were extant sister taxa. This analysis also suggested a sister-taxon relationship between *Anguis fragilis* and *Anniella pulchra* (*Anniella geronomensis* was not included in this analysis).

THE PRESENT ANALYSIS

PROCEDURES AND DATA: The matrix provided by Conrad (2008) was modified by Norell et al. (2008) to include several new taxa. Among these were the glyptosaurines *Paraplacosauriops quercyi* and *Placosaurus rugosus*, coded based on Augé and Sullivan

A   Macey et al. 1999

B   Wiens & Slingluff 2001

Heloderma suspectum
Varanus griseus
Shinisaurus crocodilurus
Xenosaurus grandis
Anniella (2 sp.)
Celestus enneagrammus
Diploglossus bilobatus
Diploglossus pleei
Ophiodes striatus
Sauresia agasepsoides
Wetmorena haetiana
Barisia imbricata
Gerrhonotus liocephalus
Abronia oaxacae
Mesaspis moreleti
Elgaria (5 sp.)
Ophisaurus koellikeri
Anguis fragilis
Pseudopus apodus
Dopasia harti
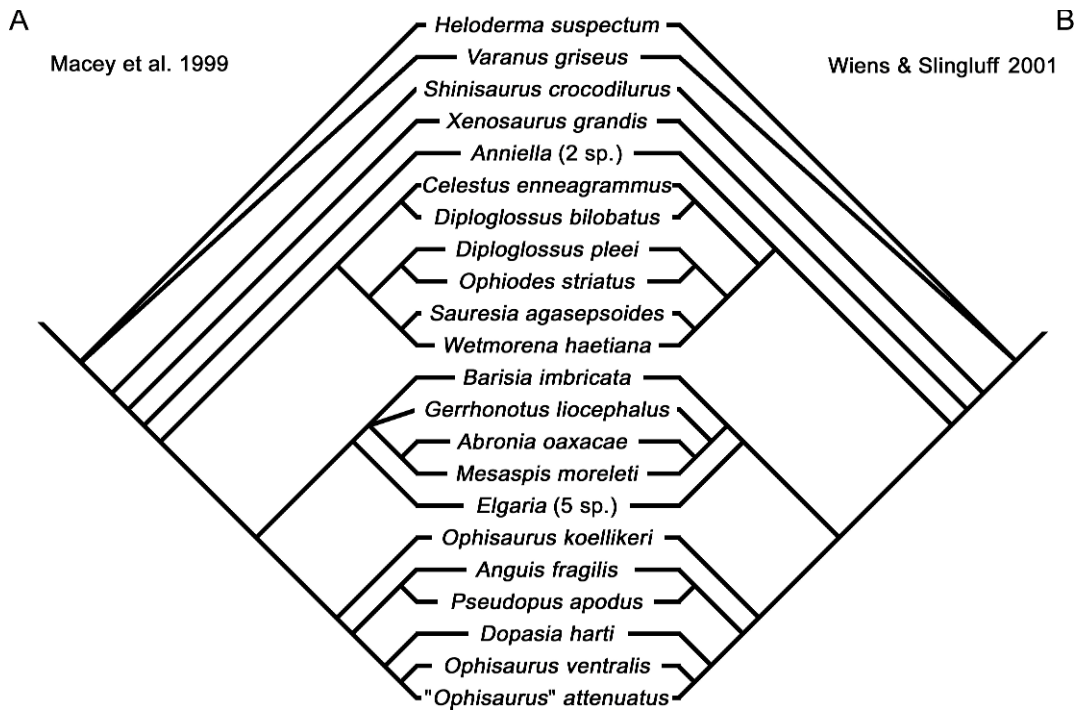*Ophisaurus ventralis*
"*Ophisaurus*" *attenuatus*

Fig. 8. Phylogenetic relationships of Anguimorpha based on molecular data as hypothesized by (A) Macey et al., 1999, and (B) Wiens and Slingluff, 2001.

(2006) and Sullivan and Augé (2006), respectively. A clade composed of Anguidae (including glyptosaurines) and Carusioidea was supported in both those analyses and the analysis undertaken by Norell et al. (2008). However, in the latter analysis, *Hymenosaurus clarki* (Late Cretaceous of Mongolia; see Gao and Norell, 2000) was vagile in its phylogenetic placement. According to that analysis it could be a basal autarchoglossan, a scincomorph, or a nested member of Anguidae (fig. 9).

Here, we conducted another analysis and limited it to carusioids and anguids. We also added *Abronia oaxacae* (Recent of southern North America; see Uetz, 2007), *Placosaurus estesi* (Middle and Upper Eocene of Europe and Asia; see Sullivan and Augé, 2006), and *Placosaurus mongoliensis* (appendix 1). *Abronia oacacae* was coded primarily from specimens (see appendix 2) with supplemental codings based on literature as described by Conrad (2008). *Placosaurus estesi* and *Placosaurus mongoliensis* were scored from Sullivan and Augé (2006). The current analy-

sis includes 37 taxa scored for 372 characters (50 of which were parsimony informative). All taxa except *Xenosaurus* were coded at the level of species. Included carusioids are *Carusia intermedia* (Late Cretaceous of Mongolia; see Borsuk-Bialynicka, 1985; Gao and Nessov, 1998; Gao and Norell, 1998), *Exostinus lancensis* (Upper Cretaceous of western United States; see Gilmore, 1928), *Exostinus serratus* (Paleocene of western United states; see Estes, 1965, 1983), *Restes rugosus* (Lower Eocene of western North America; see Gauthier, 1982), and *Xenosaurus* (Recent of southern North America; see Uetz, 2007) (coded based on *Xenosaurus grandis* and *Xenosaurus platyceps*). Data were analyzed in T.N.T. using the New Technology Search (Goloboff et al., 2003) (1,000 replicates) and three subsequent ratchet replicates (each of 1,000 replicates). We also analyzed these data using the "Traditional Search" option in T.N.T. (Goloboff et al., 2003), achieving the same result. Our analysis recovered 10 equally short trees, each with 388 steps.
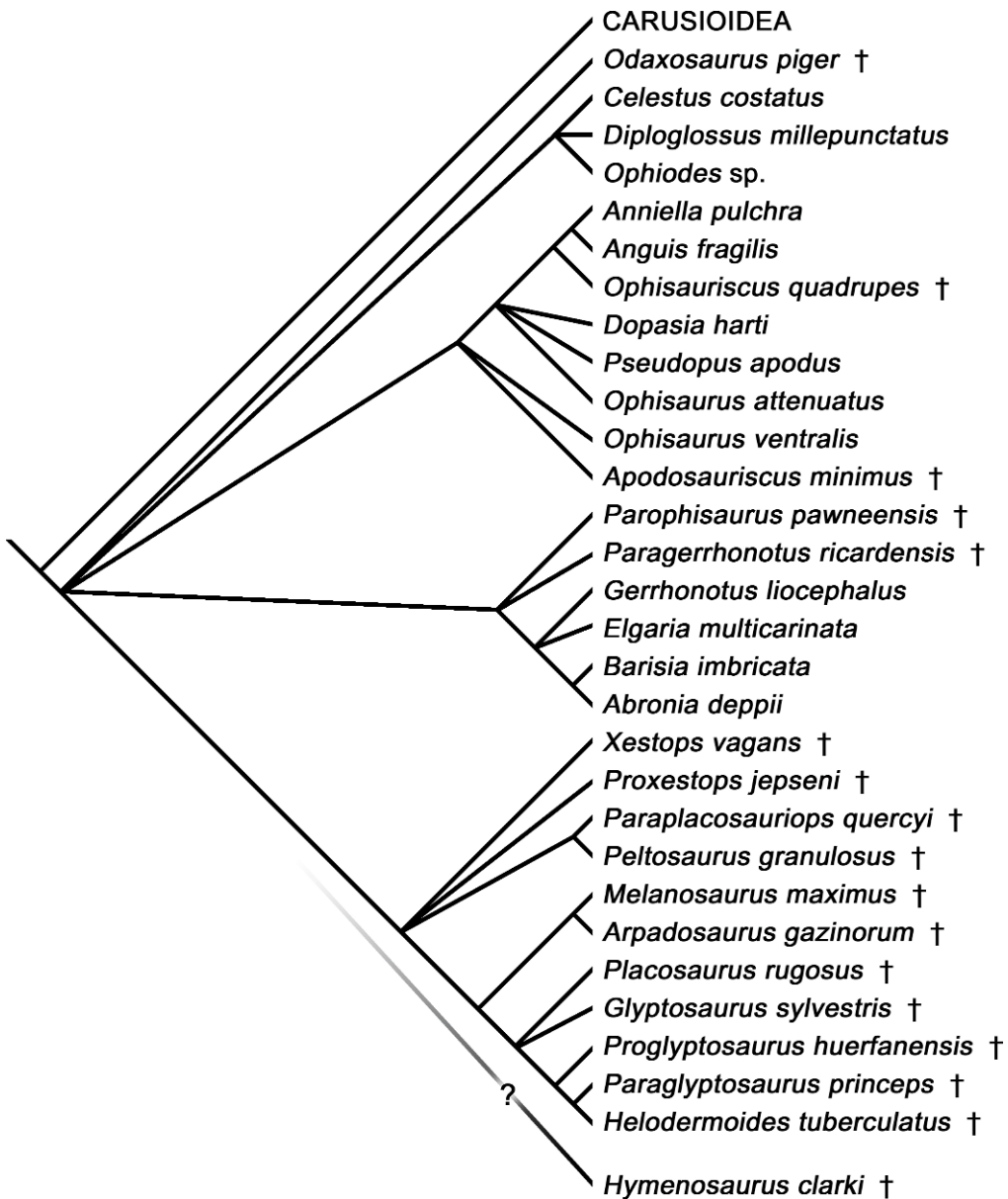
Fig. 9.   Phylogenetic relationships of anguids as based on the analysis as outlined in Norell et al. (in review); Adams consensus tree of 2,368 equally short trees. Tree length = 3,688 steps; retention index = 0.7138. Note that the placement of *Hymenosaurus clarki* is uncertain (see text).

We report both the strict consensus (fig. 10A) and the Adams consensus (fig. 10B) trees as reconstructed by PAUP* 4.0b10 (Swofford, 2001) based on the principal trees recovered in T.N.T. The Adams consensus collapses volatile taxa to their most basal recovered position and shows relationships that are consistent with all of the principle trees. We report the unambiguous synapomorphies for some of the major groups below.

We ran a third analysis including only extant carusioids (*Xenosaurus*) and anguids
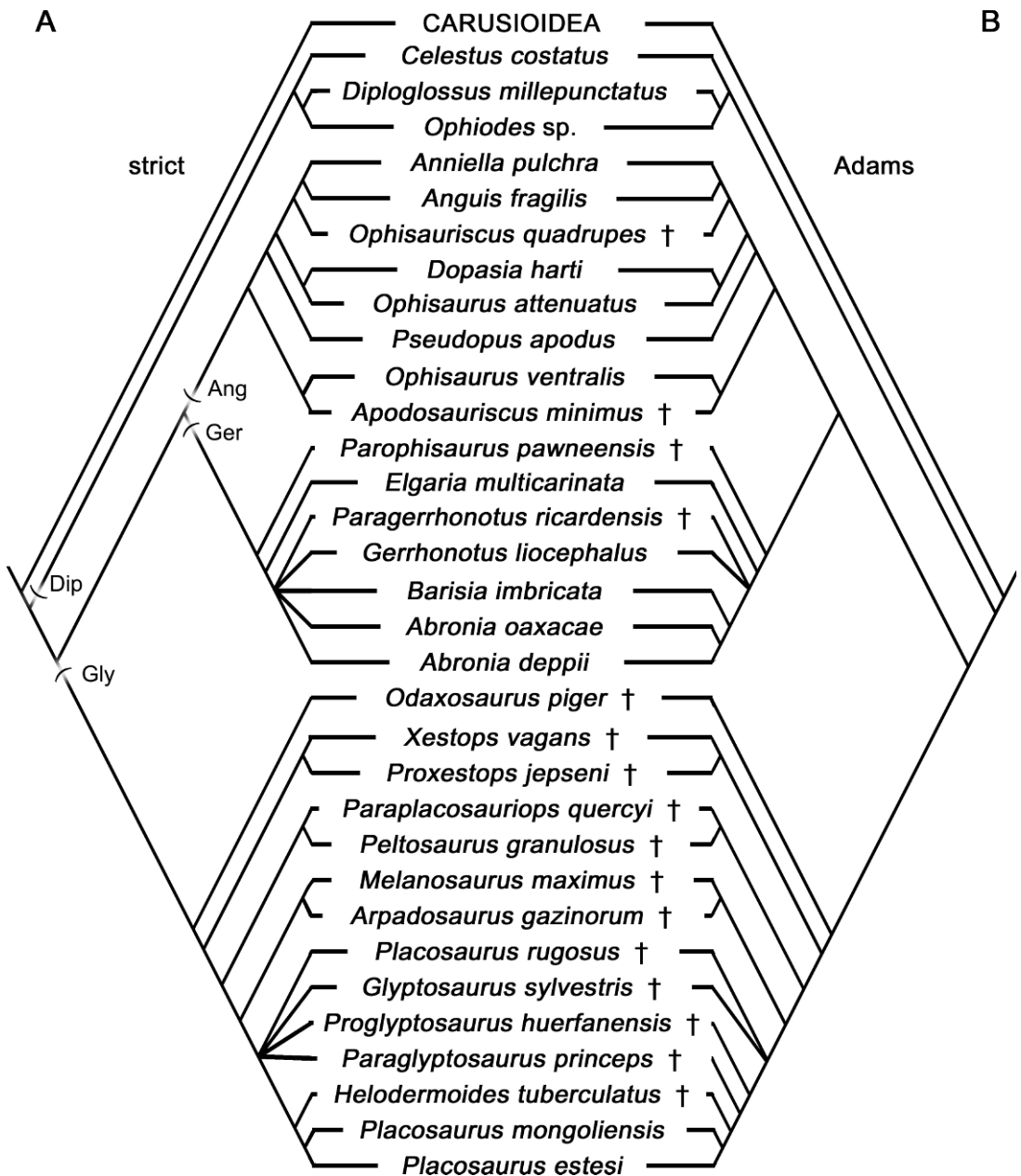
Fig. 10. Phylogenetic relationships of anguids based on the current analysis. Only carusioids and anguids were included. *Abronia oaxacae*, "*Placosaurus*" *estesi*, and "*Placosaurus*" *mongoliensis* were added to the taxa included in the Norell et al. (in review). We also added character state 3 to character 145 (see Appendix 3). (A) Strict and (B) Adams consensus of 10 most shortest recovered trees (tree length = 388; retention index = 0.6429). Abbreviations for this figure: Ang, Anguinae; Dip, Diploglossinae; Ger, Gerrhonotinae; Gly, Glyptosaurinae.

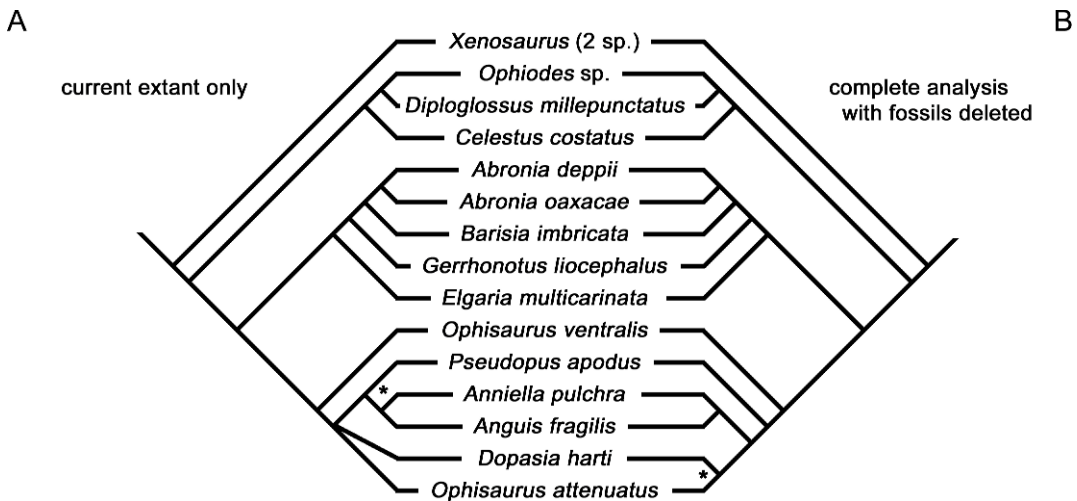Fig. 11.   Extant-only cladistic topologies of anguids, with *Xenosaurus* used as an outgroup. (A) Result of a cladistic analysis of the current data matrix when all fossil taxa are deleted before the data analyzed (tree length = 249; retention index = 0.6403). (B) The topology from the analysis presented in figure 10 with fossil taxa deleted from the tree. Asterisks identify branches that each tree shares in common with recent molecular analyses (see fig. 8) but not with the other tree topology in this figure.

for comparison with the recent molecular studies. We report the results of this analysis in figure 11.

PAROPHISAURUS PAWNEENSIS

Placement of *Parophisaurus pawneensis*: Although it has been allied previously with Anguinae, the present analysis shows *Parophisaurus pawneensis* to be a basal member of Gerrhonotinae (sensu Conrad, 2008 ; all taxa sharing a more recent common ancestor with *Gerrhonotus liocephalus* than with *Anguis fragilis*, *Anniella pulchra*, or *Diploglossus fasciatus*). This is supported by four unambiguous synapomorphies:

1. Gerrhontines plesiomorphically possess a strong medial process on the maxilla posterior and ventral to the nasal process of the premaxilla (character 26, state 1). In some taxa this strong medial process may approach and/or contact its counterpart at the midline;
2. The supratemporal process of the parietal is elongate as composed to the condition present in, for example, *Xenosaurus* (see Barrows and Smith, 1947; Rieppel, 1980) (character 88, state.1);

3. Crown striations are absent from the marginal teeth (character 219, state 0). This contrasts the condition present in some anguids such as *Pseudopus apodus*, which possess longitudinal striations radiating ventrally from the distal tip of the teeth;
4. They also possess flat body scales with a dorsal keel on the longitudinal axis of an otherwise relatively flat scale (character 312, state 1).

GERRHONOTINAE EXCLUSIVE OF PAROPHISAURUS

1. The premaxillary nasal process and the frontal interrupt the internasal contact such that they contact at the midline for less than one-half of their length (character 21, state 1);
2. The frontals are fused into a single element with the midline suture completely lost to co-ossification of the two individual elements (character 55, state 1);
3. The palatines possess a medial expansion anteriorly, distinctly constricting the pyriform recess (= interpterygoid vacuity) (character 110, state 1). This character (character 110) differs from a character

presented by Conrad (2008: character 114) to describe the presence of a secondary palate, although Estes et al. (1988) originally used a similar description to that of character 110 to describe the presence of a secondary palate;

4. Palatine teeth are absent (character 115, state 1);

5. The premaxillary teeth are similar in size to those of the anterior maxillary teeth (character 223, state 0). This condition contrasts that seen in many varanoids (e.g., *Varanus prasinus*) wherein the premaxillary teeth are markedly smaller than those in the anterior part of the maxilla.

ANGUINAE

Our analysis suggests that *Ophisaurus ventralis* and *Apodosauriscus minutus* form a clade at the base of Anguinae. This relationship is supported by the shared presence of a pair of distinct subolfactory processes on the frontal (character 61, state 1). These processes extend ventrally from the ventral surface of the frontal and partly surround the olfactory nerves.

Anguines exclusive of *Ophisaurus ventralis* and *Apodosauriscus minutus* are united by four unambiguous character states:

1. The frontals form together form a trapezoid outline when viewed in dorsal or ventral view (inaccurately termed *rhomboid* by Conrad, 2008) (character 57, state 1). That is, the frontals are broadest at the frontoparietal suture and taper more or less continuously toward the nasofrontal suture. There is no marked concavity of the lateral margins of the frontal between the orbits.

2. The quadrate possesses a relatively short tympanic crest (character 162, state 1). That is, the tympanic crest is shorter than the posterior the posterior crest of the quadrate. The latter is a somewhat arbitrary landmark for comparison used to help quantify the character states some earlier analyses (see, for example, character 51 of Lee, 1998);

3. Absence of a contact between the epicoracoid (a cartilaginous element lying ante-

rior to the coracoid and usually forming the anterior margins of the coracoid fenestrae) and the suprascapula (a cartilaginous element lying dorsal to the scapula) (character 264, state 1). Note that the scapula and suprascapula may be ontogenetically homologous in tetrapods, the demarcation between the two being determined only by the limits of ossification in the scapula (see Shearman, 2003, 2005);

4. The scapula is smaller than the coracoid (character 265, state 1). Given the proposed evolutionary trajectory hypothesized here, the size of the scapula as compared to the coracoid in this case might be interpreted as a reduction in size.

ANGUINAE EXCLUSIVE OF *PSEUDOPUS APODUS*

Anguines above the level of *Pseudopus apodus* (Recent of Europe; see Uetz, 2007) are united by four more synapomorphies;

1. Crown striations are absent from the teeth (they are present on the marginal teeth of *Pseudopus apodus*) (character 219, state 0);

2. None of the marginal teeth are chisel-shaped (character 226, state 0). Some anguids possess tooth crowns that are expanded and chisel-shaped in dorsal view. This character has been described at length by Meszoely (1970);

3. When the skull is naturally articulated and held horizontally (the resting position), the dorsal margin of the atlas is horizontally oriented (character 239, state 0), as opposed to posteroventrally inclined;

4. The pelvic elements are not sutured to one another (character 284, state 2).

"*OPHISAURUS*" *ATTENUATUS* + *DOPASIA HARTI*

"*Ophisaurus*" *attenuatus* and *Dopasia harti* form a clade exclusive of all other anguids observed in this analysis. This clade is diagnosed by three unambiguous synapomorphies:

1. Ventral processes of the frontals contact the palatines anteriorly near or at the

orbitonasal fenestra (character 67, state 1). This character does not always covary with the presence or absence of subolfactory processes (character 61), although the subolfactory processes (cristae cranii of some authors) may sometimes share a continuous outline with the anteroventral projections of the frontal that sometimes contact the palatines;

2. The pterygoid contacts the jugal posteromedial to the lacrimal and lacrimal foramen along the anteroventral margin of the orbit (character 116, state 1);

3. The atlas possesses a well-developed lateral process that partly overlaps the axis (character 240, state 0).

OPHISAURISCUS + ANGUIS + ANNIELLA

The sister group to the "*Ophisaurus*" *attenuatus* + *Dopasia harti* clade is composed of *Ophisauriscus quadrupes*, *Anguis fragilis*, and *Anniella* (represented in this analysis by *Anniella pulchra*). This nested anguine clade is diagnosed by two unambiguous synapomorphies:

1. The coronoid lacks a distinct labial flange (character 193, state 0). Some squamates (e.g., *Xenosaurus grandis*) possess a flange on the lateral/labial surface of the ascending part of the coronoid. In some taxa, this flange may be extensive and project posterolaterally beyond the level of the posterior margin of the coronoid process;

2. The marginal teeth are recurved and of a design consistent with those used in grasping and holding prey items.

ANGUIS FRAGILIS + ANNIELLA PULCHRA

Anguis fragilis and *Anniella pulchra* are further united in this analysis by seven unambiguous synapomorphies:

1. The incisive process in these taxa is a single (not bilobed) ventral projection descending from the posteromedial surface of the premaxilla (character 14, state 0);

2. The exposed anterodorsal portion of the frontal forms a wedge between the posterior parts of the nasals (character 23, state 1). This differs from the condi-

tion in many anguimorphs wherein the nasofrontal suture is not an anterior wedge, but is instead W-shaped (e.g., *Carusia intermedia* and *Varanus*);

3. The frontal possesses distinct subolfactory processes (character 61, state 1);

4. The bases of the supratemporal process do not approach each other medially, meaning that there is a transverse margin on the posterior parietal midline (character 82, state 0);

5. Unlike many anguids, which possess some mild constriction of the vertebral centrum just anterior to the posterior condyle, the vertebral centra of *Anniella* and *Anguis* are parallel-sided (character 233, state 0);

6. *Anguis fragilis* and *Anniella pulchra* lack a functional sacrum (character 247, state 1). This is convergent with the condition in *Pseudopus apodus* based on the current phylogenetic hypothesis;

7. There is no lateral fold on the body as is often present in anguids such as *Pseudopus apodus* and gerrhonotines (character 304, state 0).

PHYLOGENETIC PLACEMENT OF GLYPTOSAURINAE

Glyptosaurines are nested within crown-group anguids, being the sister taxon to a clade composed of Gerrhonotinae and Anguinae. The position of Glyptosaurinae as sister taxon to the gerrhonotine-anguine clade is supported by six unambiguous synapomorphies:

1. The dorsal margins of the supratemporal processes of the parietal are broad and flattened, a condition that is convergent with some monstersaurs (character 81, state 1);

2. Palatine and pterygoid teeth are present in patches (characters 115 and 118, state 0 in each);

3. The dentary partly encircles the anterior inferior alveolar foramen, contributing to the dorsal and anterior borders (character 183, state 2);

4. Known caudal vertebrae possess double transverse processes that converge distally (character 251, state 2);

5. A lateral fold is present, separating the dorsal battery of osteoderms from the lower battery (character 304, state 1) and presumably allowing expansion of the

body during breathing while maintaining the integrity/stiffness of the armor.

GLYPTOSAURINE SYNAPOMORPHIES

Glyptosaurinae (sensu Conrad, 2008; all taxa sharing a more recent common ancestor with *Glyptosaurus sylvestris* than with *Anguis fragilis*, *Diploglossus millepunctatus*, or *Gerrhonotus liocephalus*) is diagnosed by three unambiguous character states

1. Distinct subolfactory processes are present on the frontal (character 61, state 1);
2. The bases of the supratemporal process do not approach each other medially, meaning that there is a transverse margin on the posterior parietal midline (character 82, state 0);
3. The marginal teeth possess squared-off dorsal margins (character 212, state 6).

NON-*ODAXOSAURUS* GLYPTOSAURINAE

Odaxosaurus piger is recovered as the most basal glyptosaurine. Glyptosaurines exclusive of *Odaxosaurus piger* are united by four unambiguous synapomorphies:

1. The dermal sculpturing of dermal skull elements is pitted (character 7, state 1);
2. The maxilla bears dermal sculpturing (character 8, state 1);
3. The posteroventral margin of the intramandibular septum (see Meszoely, 1970; Rieppel and Zaher, 2000) is sutured to the medial surface of the main body of the dentary (character 311, state 2); that is, it is not a free flange;
4. Body osteoderms and/or scales with distinct vertical keels (character 312, state 1).

PROXESTOPS JEPSENI + *XESTOPS VAGANS*

Proxestops jepseni and *Xestops vagans* (Middle Eocene of western United States) form the sister group to a clade containing *Peltosaurus granulosus*, *Paraplacosauriops quercyi*, melanosaurins (of current usage; see below), and glyptosaurins. The clade *Proxestops jepseni* + *Xestops vagans* is supported by the presence of a dentary contribu-

tion to the margin of the anterior surangular foramen (character 173, state 2).

HIGHER GLYPTOSAURINAE

Glyptosaurines exclusive of *Proxestops jepseni* and *Xestops vagans* are united by four unambiguous synapomorphies:

1. The frontals are fused (co-ossified) into a single element (character 55, state 1);
2. Increased contact is present between the parietal and the elements of the supratemporal arch, constricting or closing the supratemporal fenestra (character 84, state 1);
3. Close proximity of the anterior openings of the Vidian canals ventral to the parasphenoid rostrum (character 145, state 3; see appendix 1);
4. Posterior extension of the intramandibular septum relative to the dentary tooth row (character 170, state 0).

Within this clade, *Peltosaurus granulosus* and *Paraplacosauriops quercyi* form a clade diagnosed by the shared presence of a ventrally arched dentary (character 178, state 1).

MELANOSAURINI + GLYPTOSAURINI

The *Peltosaurus granulosus–Paraplacosauriops quercyi* clade is the sister taxon to a melanosaurin-glyptosaurin clade, which is diagnosed by two unambiguous synapomorphies:

1. The frontal unit is trapezoidal in shape (character 57, state 1);
2. The postfoveal crests (cristae postfovealis of Klembara, 1979, 1981, 1986) meet at the midline on the ventral surface of the parietal and close the parietal fossa posteriorly.

MELANOSAURINI (SENSU STRICTO)

We find a sister group relationship between *Melanosaurus maximus* and *Arpadosaurus gazinorum* (Lower Eocene of western United States; see Meszoely, [1970]; Estes, [1983]); thus the name Melanosaurini (sensu stricto) may be applied to this clade. Melanosaurins are united by the shared presence of an

anteroposteriorly elongate supratemporal (character 88, state 1).

GLYPTOSAURINI

Glyptosaurini is a distinctive clade within Glyptosaurinae. In this analysis, glyptosaurins are an unresolved trichotomy between *Glyptosaurus sylvestris* (including *Glyptosaurus princeps* and *Glyptosaurus* [*Paraglyptosaurus*] *hillsi*; Sullivan, 1986, 1989), *Placosaurus rugosus*, and higher glyptosaurins. This clade is supported by five unambiguous synapomorphies:

1. Dermal rugosities are present on the postorbital process of the jugal (character 50, state 1);
2. The supratemporal processes of the parietal are relatively short, less than 1/2 of the length of main body of parietal (character 80, state 1);
3. The dentary contributes to the dorsal, but not the anterior margin of the anterior inferior alveolar foramen (character 183, state 1);
4. The cephalic osteoderms are relatively small, not developed as head shields (character 298, state 1);
5. The cephalic osteoderms are developed as thickened mounds (character 310, state 2).

PROGPLYPTOSAURUS HUERFANENSIS + HIGHER GLYPTOSAURINS

The strict consensus also collapses *Proglyptosaurus huerfanensis* (Lower Eocene of western United States) and *Paraglyptosaurus princeps* (Lower Eocene of western North America; see Sullivan, 1979) into the basal glyptosaurin polychotomy, but the Adams consensus tree places these taxa as successively more proximal outgroups to a clade containing *Helodermoides tuberculatus*, "*Placosaurus*" *estesi*, and "*Placosaurus*" *mongoliensis*. The clade *Proglyptosaurus huerfanensis* + higher glyptosaurins is united by two unambiguous synapomorphies:

1. The jugal is not angulated; instead it is curved (character 47, state 1);
2. There is no posteroventral jugal process (character 48, state 1).

THE HELODERMOIDES LINEAGE

The clade containing *Paraglyptosaurus princeps*, *Helodermoides tuberculatus*, "*Placosaurus*" *estesi*, and "*Placosaurus*" *mongoliensis* is diagnosed by two unambiguous synapomorphies:

1. Absence of increased contact between the parietal and supratemporal arch (character 84, state 0; interpreted here as a reversal of one of the synapomorphies joining glyptosaurines above the level of *Xestops vagans* and *Proxestops jepseni*);
2. None of the marginal teeth are chisel-shaped (character 226, state 0).

Helodermoides tuberculatus is the sister taxon to "*Placosaurus*" *estesi* and "*Placosaurus*" *mongoliensis* in a clade diagnosed by the presence of two distinct (unfused) frontal (character 55, state 0). "*Placosaurus*" *estesi* and "*Placosaurus*" *mongoliensis* are united based on the shared presence of concave lateral margins of the frontals (character 57, state 2). "*Placosaurus*" *estesi* and "*Placosaurus*" *mongoliensis* cannot be diagnosed from each other based on the data used here.

EXTANTS-ONLY ANALYSIS

The extant-only analysis recovers a topology that differs from that described above in the placements of some anguines (fig. 11). The extant-only topology (fig. 11A) was more similar to recent molecular-based hypotheses in suggesting a close relationship between *Anguis fragilis* and *Pseudopus apodus*. The topology of extant taxa from the analysis described above (with fossils simply omitted from the figure) was more similar to the molecular tree in recovering a clade including *Dopasia harti* and *Ophisaurus attenuatus* to the exclusion of *Anguis* (fig. 11B). Note that *Anniella pulchra* always remains the sister taxon to *Anguis fragilis* in these analyses.

DISCUSSION

SKULLS OF GLYPTOSAURINES: Osteoderms and partial skulls are the elements most often recovered for Glyptosaurinae. Glyptosaurine braincases are rare and reasonably complete ones are preserved only in *Glyptosaurus*

sylvestris, *Helodermoides tuberculatus*, *Melanosaurus maximus*, and *Peltosaurus granulosus*. These glyptosaurine braincases are largely conservative with respect to those of other anguids. However, the specimens of *Melanosaurus maximus* and *Helodermoides tuberculatus* examined here reveal distinctive features in their braincase morphology; the basipterygoid processes are located near the midline, and anterior openings to the Vidian canal lie ventral to the parasphenoid rostrum. The robustness of the basipterygoid processes with their near absence of a constricted neck, their proximity to one another near the midline (and concomitant narrowing of the interpterygoid vacuity), and the unusual arrangement of the parasphenoid rostrum and Vidian canal may be related.

It is surprising that this novel braincase morphology was undetected previously given the history of publications addressing some or all of the specimens included in this study (Camp, 1923; Gilmore, 1928; McDowell and Bogert, 1954; Meszoely, 1970; Sullivan, 1979; Estes, 1983). One possible explanation for this is the state of preservation of the material. Available braincases of *Melanosaurus maximus* are damaged and the braincase of *Helodermoides tuberculatus* (AMNH FR 6800) was previously misidentified and mislabelled. *Glyptosaurus sylvestris* also shares this unusual morphology (visible in Sullivan, 1986: fig. 4) as does *Peltosaurus granulosus* (AMNH FR 42915).

ANGUID PHYLOGENY: The current phylogenetic hypothesis differs significantly from those of Sullivan (1979) and Gauthier (1982). It is similar to recent molecular studies (Macey et al., 1999; Wiens and Slingluff, 2001) (fig. 8) in suggesting that Diploglossinae is relatively basal within Anguidae.

Anniella has been a problematic taxon. It shows significant similarities with *Anguis fragilis*, but these have been dismissed as convergences based on similar lifestyles (Gauthier, 1982) and molecular data suggest that it is not closely related to anguines (Macey et al., 1999; Wiens and Slingluff, 2001) (fig. 8). Even so, all morphology-based cladistic analyses have suggested a close relationship between *Anguis* and *Anniella* (Rieppel, 1980; Gao and Norell, 1998; Conrad, 2008). Shared ancestry and shared ecology/lifestyle are not mutually exclusive; that is, presumably a hypothetical burrowing ancestor of *Anguis* might also have given rise to an even more fossorial *Anniella*. The possibility of a long-missing lineage between *Anguis* and *Anniella* (see below) raises the issue of potential long-branch attraction in the molecular data set, in the morphological data set, or in both. Unfortunately, there is little in the way of fossil record for either *Anniella* or *Anguis* prior to the Middle Miocene (see Bell and Mead, 1995, and Bell and Whistler, 1996, for Miocene and Pleistocene records of anniellines), so transitional morphologies are lacking.

Apodosauriscus minutus (Wasatch Formation, Lower Eocene; see Gauthier, 1982) has been suggested as a sister taxon to *Anniella* (Gauthier, 1982; Estes, 1983). The holotype for *Apodosauriscus minutus* is "the posterior one-half of [a] left dentary" (Gauthier, 1982: 14) that shows some similarity to *Anniella*. We have accepted Gauthier's (1982) referral of several specimens (including dentaries and maxillae) to *Apodosauriscus minutus* and included it in this analysis. The current data suggest that *Ophisaurus ventralis* is the sister taxon to *Apodosauriscus minutus* (see the systematics section above). More complete remains may clarify the phylogenetic position of this problematic taxon.

Our analysis confirms a nested position of *Peltosaurus granulosus* within Glyptosaurinae, contra Conrad (2006). The Melanosaurini of traditional usage (see Sullivan, 1979; Estes, 1983; Sullivan, 1986, 1989; Augé and Sullivan, 2006; Sullivan and Augé, 2006) is demonstrated as paraphyletic with respect to the monophyletic Glyptosaurini. *Odaxosaurus piger* is the basalmost known glyptosaurin (sensu Estes, 1983, but not Sullivan, 1986). The remaining six melanosaurins considered in this study represent three small radiations ranging in age from the Late Paleocene to the Oligocene. *Placosaurus* sensu Sullivan and Augé (2006) is paraphyletic with respect to other glyptosaurins. "*Placosaurus*" *mongoliensis* ("middle Eocene" of Asia as described by Sullivan and Augé, 2006: 131) and "*Placosaurus*" *estesi* ("latest middle Eocene" of Europe as described by Sullivan and Augé, 2006: 129) form a clade that is the sister taxon to the North American *Helodermoides tuberculatus*.

ANGUID EVOLUTION AND BIOGEOGRAPHY: *Odaxosaurus piger*, the earliest known anguid, comes from the Late Cretaceous of United States [*Bainguis parvus* is a non-anguimorph scleroglossan (Conrad, 2008)]. Carusioids, the sister group to anguids in this and recent morphology- and molecular-based studies (Conrad, 2008, and Townsend et al., 2004, respectively), also appear in the Late Cretaceous. Given the current phylogenetic hypothesis, three other anguid lineages must have been present by that time (diploglossines, at least stem members of the gerrhonotine-anguine clade, and the lineage leading to other glyptosaurines). Another relatively basal glyptosaurine, *Proxestops jepseni*, comes from the mid- to late Paleocene, whereas the greatest diversity of the clade is known from the Eocene.

Anguids are known only from western North America prior to the Eocene. Anguid fossils are known from Europe by the end of the Middle Eocene (the anguine *Ophisauriscus quadrupes* from Germany, and the glyptosaurines *Paraplacosauriops quercyi*, *Placosaurus rugosus*, and "*Placosaurus*" *estesi* from France; see Sullivan et al., 1999; Augé and Sullivan, 2006; Sullivan and Augé, 2006). The hypothesized sister taxon to "*Placosaurus*" *estesi*, "*Placosaurus*" *mongoliensis* is known from the Late Eocene of eastern Asia. Given the presence of isolated skeletal elements from northern regions (Meszoely and Ford, 1976; Estes and Hutchison, 1980), it is clear that anguids were using polar or near-polar dispersal routes offered by the relatively equable Eocene climate. *Paraplacosauriops quercyi* (France) and *Peltosaurus granulosus* (western United States) are sister taxa. The presence of the nested Middle Eocene anguine *Ophisauriscus quadrupes* also helps to explain the far-flung distribution of extant anguines. It may also suggest that the *Aniella*- and *Anguis*-lineages were distinct by the Late Eocene, helping to account for the great geographic separation of these apparently closely related taxa.

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APPENDIX 1

ADDITION TO THE DATA MATRIX

ADDITIONAL CHARACTER STATE

We have added one character state to character 145. Thus, character 145 now reads: Sphenoid, anterior opening of Vidian canal (NG-18): (0) ventral to dorsum sella; (1) in the floor of the braincase, dorsal to the dorsum sella; (2) opens on the ventral surface of the parabasisphenoid (from Wiens and Etheridge, 2003); (3) anteriorly oriented and lying near the midline, ventral to the parasphenoid rostrum.

This character (145) is coded as it was in Conrad (2008) and Norell et al. (2008) with the following exceptions: State 2 occurs in *Hoplocercus spinosus* and state 3 occurs in *Glyptosaurus sylvestris*, *Helodermoides tuberculatus*, *Melanosaurus maximus*, and *Peltosaurus granulosus*.

ADDITIONAL TAXA

We have added three taxa to the data matrix provided by Conrad (2008) and Norell et al. (2008) (both available for free download from http://digitallibrary.amnh.org/dspace/).

AbroniaOAX

100000000011110000000010300100001100000010100-00000000000011020000?0?01100101100100001000001-011000100110011000100111001010021000100000-0000000020000010011000001100???11?00001000??01-00001000011100000010010000??00?1011020200000-000100000???120?????00???1?????????????????????????-????????????????????????????2???????????????????????-??3000??010???0-10?0????0?

PlacoMONGOL

?????1??1??????????30?????????0??????????????0-02000100??1?0?101??????????????????????????????-???-???-???-??????????????????1?????1????22?????????????????-????????????????????????????8?????????1???????0?

PlacoESTESI

?????1??1????????????30?????????0??????????????-002000100??1?00101??????????????????????????????-???-???-???-??????????????????1?????1????22?????????????????-????????????????????????????4?????????????????0?

APPENDIX 2

SPECIMENS USED FOR CODING MORPHOLOGY

Here we list the anguids, carusioids, and shinisaurids used directly for the limited analysis presented here (see fig. 10). For other squamates used for the more inclusive analysis, please see Conrad, 2008, and Norell et al., 2008.

Institutional abbreviations: AMNH, American Museum of Natural History; FMNH, Field Museum of Natural History; UF, University of Florida, Florida State Museum.

Abronia deppii FMNH 38523; *Aiolosaurus oriens* IGM 3/171; *Anguis fragilis* AMNH R56193; *Anniella nigra* FMNH 213666; *Bahndwivici ammoskius* FMNH PR 2260; *Barisia imbricatus* FMNH 6526, FMNH 6528; *Carusia intermedia* IGM 3/18, IGM 3/22, IGM 3/23, IGM 3/26; *Celestes costatus* FMNH 13254; *Clidastes propython* FMNH PR 38, FMNH P27324; *Diploglossus millepunctatus* FMNH 19248; *Dopasia harti* FMNH 24298; *Elgaria* sp. FMNH 23235, FMNH 213397; *Gerrhonotus liocephalus* FMNH 22452; *Helodermoides tuberculatus* AMNH FR5902, AMNH FR6800, AMNH FR8706; *Melanosaurus maximus* AMNH FR5168, AMNH FR5175; *Ophisaurus attenuatus* FMNH 98466, FMNH 98467, FMNH 207671; *Ophiodes* sp. FMNH 9270; *Paraglyptosaurus princeps* AMNH FR6055; *Peltosaurus granulosus* AMNH FR42913, AMNH FR42915, AMNH FR1710, AMNH FR8138, FMNH P27072, FMNH UC391, FMNH UC1720; *Pseudopus apodus* FMNH 216745, FMNH 22088, FMNH 22359; *Shinisaurus crocodilurus* FMNH 233130, FMNH 234242; UF 57112,

UF 61149, UF 61685, UF 62315, UF 62316, UF 62497, UF 62536, UF 62578, UF 68203; *Xenosaurus grandis* FMNH 211833; *Xenosaurus platyceps* UF 43396, UF 43397, UF 45590, UF 53691, UF 56122.

APPENDIX 3

ANATOMICAL ABBREVIATIONS IN FIGURES

aab	anterior auditory bulla
avc	anterior opening of the Vidian canal
bpt	basipterygoid process
cal	crista alaris
cc	cranial carotid canal
cpr	crista prootica
crtr	crista trabecularis
csel	crista sellaris
foo	fenestra ovalis
fso	facet contacting the supraoccipital
ipr	inferior process
L	left
oc	occipital condyle
ocr	occipital recess
poc	paroccipital process
ps	parasphenoid rostrum
pvc	posterior opening of the Vidian canal
R	right
sot	spheno-occipital tubercle
VI	path of the abducens nerve (cranial nerve VI)
X	path of the vestibulocochlear nerve (cranial nerve X)
XII	path of the hypoglossal nerve (cranial nerve XII)